



Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification

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ARTICLE INFO

Article history:

Received 1 July 2011

Revised 7 November 2011

Accepted 26 November 2011

Available online xxxx

Keywords:

Mutualism

Co-speciation

Pollination

Tegeticula

Prodoxus

ABSTRACT

Coevolution is thought to be especially important in diversification of obligate mutualistic interactions such as the one between yuccas and pollinating yucca moths. We took a three-step approach to examine if plant and pollinator speciation events were likely driven by coevolution. First, we tested whether there has been co-speciation between yuccas and pollinator yucca moths in the genus *Tegeticula* (Prodoxidae). Second, we tested whether co-speciation also occurred between yuccas and commensalistic yucca moths in the genus *Prodoxus* (Prodoxidae) in which reciprocal evolutionary change is unlikely. Finally, we examined the current range distributions of yuccas in relationship to pollinator speciation events to determine if plant and moth speciation events likely occurred in sympatry or allopatry. Co-speciation analyses of yuccas with their coexisting *Tegeticula* pollinator and commensalistic *Prodoxus* lineages demonstrated phylogenetic congruence between both groups of moths and yuccas, even though moth lineages differ in the type of interaction with yuccas. Furthermore, *Yucca* species within a lineage occur primarily in allopatry rather than sympatry. We conclude that biogeographic factors are the overriding force in plant and pollinator moth speciation and significant phylogenetic congruence between the moth and plant lineages is likely due to shared biogeography rather than coevolution.

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1. Introduction

Obligate mutualism poses a conundrum for evolutionary biology for two reasons. First, mutualistic interactions are antagonistic interactions in which the fitness benefits outweigh the fitness costs, and the net benefits and costs may shift depending on ecological conditions (Thompson and Pellmyr, 1992; Bronstein, 1994). For example, in mutualisms involving seed-eating pollinators, plants pay a cost in terms of loss of offspring, but this cost is outweighed by a larger fitness gain through increased pollination and seed production. Evolutionary theory predicts that over time natural selection should act on mutualists to maximize fitness benefits and minimize fitness costs (Trivers, 1971; Axelrod and Hamilton, 1981; Murray, 1985; Bull and Rice, 1991; Doebeli and Knowlton, 1998; Herre et al., 1999; Weiblen et al., 2001; Bronstein, 2001; West et al., 2002; Holland et al., 2002), and mutualism is likely to break down without regulatory mechanisms that prevent overexploitation (Sachs and Simms, 2006; Edwards et al., 2010; Jandér and Herre, 2010). In spite of these regulatory mechanisms, cheaters/exploiters have evolved from within mutualistic lineages

(Addicott, 1996; Pellmyr et al., 1996; Pellmyr and Leebens-Mack, 2000; Segraves et al., 2008). The second reason is that obligate mutualism usually results in extremely specialized interactions. Although not always true, specialization has been suggested to be an evolutionary dead-end because it increases the likelihood of extinction (Kelley and Farrell, 1998; Tripp and Manos, 2008; Johnson, 2010). For obligate mutualists, extinction of one mutualist leads to the extinction of the other. Despite the results from theoretical models and the assumption that specialization is a dead-end, some obligate mutualisms such as those between yuccas and yucca moths, figs and fig wasps, and attine ants and fungi have persisted for tens of millions of years (Pellmyr and Leebens-Mack, 1999; Mueller et al., 2001; Rønsted et al., 2005). Furthermore, once started, these mutualisms have diversified into species complexes of interacting mutualists whose evolutionary histories and futures are intricately linked (Pellmyr, 2003; Jousselin et al., 2006).

Obligate mutualisms are a small subset of mutualistic interactions, but they provide excellent systems to test ideas about the role of coevolution in mutualism. One of the unanswered questions in mutualism is the degree to which coevolution, reciprocal evolutionary change between mutualists, can be a significant factor in causing reproductive isolation, speciation, and cladogenesis. For

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example, once an obligate mutualism is established and coevolution has molded the mutualists, does subsequent diversification of the interacting lineages demonstrate that ongoing coevolution is the driver? Answering this question in a phylogenetic framework is often difficult because there are a number of possible outcomes in phylogenetic patterns that could be generated by coevolution (Thompson, 1994, 2005; Segraves, 2010), and coevolution may have been important in some diversification events but not all lineages within a group. Co-speciation analyses have been widely used as a starting point to assess the potential importance of coevolution in diversification, but co-speciation between interacting lineages does not necessarily imply that reciprocal evolutionary change was the causative agent. Interacting mutualistic species will experience the same biogeographic and climatic events that may cause allopatric divergence in both lineages as a mutualistic interaction spreads across the landscape (Smith et al., 2008a). A pattern of co-speciation, then, can be generated by multiple processes making it imperative to differentiate among them in order to determine the major factor driving diversification.

We address the importance of coevolution to diversification in the obligate pollination mutualism between yuccas and yucca moths (reviewed in Pellmyr, 2003). This mutualism is often considered a classic example of coevolution and diversification (Rose and Mueller, 2006; Ricklefs, 2010). The mutualism has persisted for over 40 million years and has lead to interacting species complexes of plants and moths that are distributed across North America (Pellmyr and Leebens-Mack, 1999). The genus *Yucca* is the host plant for the yucca moths and consists of three monophyletic sections that differ in fruit type: the capsular-fruited *Chaenocarpa*, the fleshy-fruited *Sarcocarpa*, and the spongy-fruited *Clistocarpa* (McKelvey, 1938, 1947; Clary, 1997; Pellmyr et al., 2007). *Yucca* species range in size from small rosettes to large, towering plants, but all produce one or more inflorescence stalks that hold ten to several hundreds of flowers, and all are pollinated by yucca moths.

There are two genera of pollinator moths, *Tegeticula* and *Parategeticula*, in which female moths use unique mouthparts referred to as maxillary tentacles to actively collect and deposit pollen on the yucca flower stigmas (Riley, 1892; Davis, 1967; Pellmyr, 2003). Females lay eggs in the yucca flower, and moth species differ in how they place their eggs in the floral tissues. Among the 20 known species of *Tegeticula*, some species lay eggs deep into the locule next to developing ovules, and others lay eggs superficially in the outer pistil wall (Pellmyr, 2003). There are also two cheater species that feed on seeds but do not pollinate (Pellmyr et al., 1996; Pellmyr and Leebens-Mack, 1999, 2000). In contrast, the five *Parategeticula* species lay eggs in shallow pits excavated in the flower petiole or petal, and after hatching, the larva crawls to the developing fruit to feed on seeds. Because moth larvae of all pollinator species only consume a small fraction of the developing seeds, the interaction is mutualistic for both moths and plants. The complete life cycle of the moth is tied to its host, with mating occurring on the host plant, and larvae and adults feed on no other plants. There are no co-pollinators of yuccas. Plant reproduction is thus completely dependent on yucca moth pollination.

In addition to the pollinator moths, yuccas are also used by a genus of closely related moths, *Prodoxus*, all of which feed on inflorescence tissue, with the exception of one species that is a leaf miner. Like the pollinator species, the complete life cycle of these moths is tied to the host. Individuals mate on the host plant but do not pollinate. Larvae feed and pupate within plant tissues; however, they do not feed on yucca seeds. Of the 17 described *Prodoxus* species that use yuccas, ten species feed within the interior of the inflorescence stalk, six species feed within cysts at the base of the developing fruit, and one species has transitioned to a leaf miner feeding style. Ecological work demonstrates that *Prodoxus* has minimal to no impact on plant fitness (Bronstein and Ziv, 1997; Althoff et al., 2004).

The radiations of *Tegeticula*, *Prodoxus*, and *Yucca* provide a comparative template to examine whether the coevolving mutualistic interaction between pollinators and yuccas is responsible for diversification in moth and plant lineages. Although members of the non-pollinating *Prodoxus* lineage are also extreme specialists on yuccas, they are commensalists. Thus, *Prodoxus* is unlikely to coevolve with yuccas, unlike the pollinator moths, because there is no reduction in plant fitness due to *Prodoxus* feeding. Consequently, examining co-speciation of *Prodoxus* with *Yucca* provides an ecological contrast to help determine the role of coevolution in co-speciation between *Tegeticula* and yuccas. These sister lineages of moths have similar levels of intimacy with their hosts, but differ in the type of interaction and propensity to coevolve with yuccas. We use previously published phylogenies of *Yucca* and *Tegeticula*, and supplemented a mtDNA phylogeny of *Prodoxus* to examine patterns of host use and speciation within moth lineages and to compare patterns of speciation between the interacting groups. Given the differences in selection pressures applied by pollinators in the genus *Tegeticula* relative to commensalistic *Prodoxus* moths, we predict that *Tegeticula* would exhibit a stronger pattern of co-speciation with their yucca hosts. Alternatively, if speciation within *Tegeticula* is largely due to geographic isolation as a result of range expansion and historical biogeography as opposed to coevolution, we would expect both pollinator and non-pollinator lineages to have similar patterns of phylogenetic congruence with yuccas.

2. Methods

Phylogenetic data from Althoff et al. (2006), Pellmyr et al. (2006), Pellmyr et al. (2007) and Pellmyr et al. (2008) were supplemented with new mtDNA cytochrome oxidase I and II sequences of a new species of *Prodoxus*, *P. praedictus*, that feeds within the fruit of *Y. schidigera* (GenBank Accession number GQ981319) (Pellmyr et al., 2009). These data included 4322 AFLP markers for the genus *Yucca*, and 2105 bp of mtDNA cytochrome oxidase I and II for the moth genera. A single individual was chosen to represent each species with the exception of *Tegeticula corruptrix*, which is the only moth species that feeds on both fleshy and capsular-fruited yuccas. A more extensive phylogeographic analysis suggests populations of *T. corruptrix* feeding on fleshy and capsular-fruited yuccas may constitute distinct lineages (Segraves et al., unpublished). We used one individual from each lineage. Methods for sequencing followed those in Althoff et al. (2006).

2.1. Phylogenetic analyses

The *Yucca* AFLP data were used in a Bayesian analysis implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) to estimate the plant phylogeny. *Hesperoyucca whipplei* was used as the outgroup. We chose one representative individual for each species except for *Y. brevifolia*, where emerging data suggest that *Y. brevifolia* may be two species situated along a north–south transect in the Mojave desert region (Pellmyr and Segraves, 2003; Godsoe et al., 2008; Smith et al., 2008a,b). For *Y. brevifolia*, we used one representative each from the northern and southern lineages. Bayesian analysis parameters included a restriction site model with Iset coding = no absencesites, two runs with four chains, with relative burnin of 0.25, 4 million generations, and sampling every 1000 generations.

Moth sequence data were analyzed with both maximum likelihood and Bayesian methodologies. The analyses included *Prodoxus* (22 species), *Parategeticula* (5 species) and *Tegeticula* (20 species) (Supplemental Table 1). *Mesepiola specca* (U49022) was used as the outgroup. The model of sequence evolution was determined using DT-ModSel (Minin et al., 2003). GTR + I + G was identified

as the most likely model of sequence evolution with the following model parameter estimates: rate matrix = (4.783, 21.205, 7.854, 6.733, 62.251) base frequencies = (0.329, 0.110, 0.127), proportion of invariable sites = 0.511, and gamma shape = 0.885. Maximum likelihood analyses were implemented in PAUP 4.0b10 using a heuristic search with random sequence addition and TBR branch swapping. One hundred nonparametric bootstrap replicates were performed to assess support for the resulting nodes (Felsenstein, 1985). MrBayes3.1.2 was used for the Bayesian analyses. Parameters included a sequence evolution model of lset nst = 6, rates = invgamma, two runs with four chains, with relative burnin of 0.25, 4 million generations, and sampling every 1000 generations.

2.2. Comparisons of plant and moth phylogenies

Moth host use patterns were collated from Pellmyr (1999), Althoff et al. (2006), Pellmyr et al. (2006), and Pellmyr et al. (2007). We examined the possibility of co-speciation and host switching in three ways. First, we examined host use in relation to the moth phylogeny to determine if, in general, there is a pattern of conserved host associations with groups of closely related moths feeding on group of closely related plants. Second, we performed ParaFit analyses (Legendre et al., 2002) on the *Tegeticula* and the *Prodoxus* phylogenies obtained from the maximum likelihood and Bayesian analyses and the phylogeny of *Yucca* obtained from the Bayesian analysis. We used the patristic distances as the distance matrices for the moths and plants and conducted 1000 replicates for statistical testing. We did not include an analysis for *Parategeticula* because of its limited number of extant species (Supplemental Table 1; Pellmyr et al., 2008). For *Tegeticula* and *Prodoxus*, we only included the clades in both lineages that feed on *Yucca*. Third, we used JANE (Conow et al., 2010), an event-based method, to examine co-speciation. We performed analyses with 500 generations and population sizes of 100. We explored how changes in the cost structure associated with co-speciation, duplications of parasites, host switches, loss of parasites, and failure to diverge changed the overall costs of co-speciation between plant and moth lineages. Although there are several other possible methods to compare phylogenies of two lineages (summarized in Hughes et al., 2007), there are two confounding factors that preclude the use of many of these methods in comparisons of yuccas and their associates: some moth species use multiple hosts, and parts of the phylogenies of moths and plants are poorly resolved. Given these conditions, we chose to compare the phylogenies of plants and moths using ParaFit and JANE because these are co-speciation tests that can account for these confounding factors.

2.3. Range overlap analysis in *Yucca*

We estimated the current range distributions for the *Yucca* species with known *Tegeticula* pollinator species. *Yucca* range distributions were compiled from previously published systematic revisions of the moths (Pellmyr, 1999; Pellmyr et al., 2006) and collection notes by each of the authors. These ranges were drawn in ArcGIS (version 9.2) and range size in hectares was calculated. The degree of range overlap between all pairs of *Yucca* species within the fleshy-fruited and capsular-fruited lineages was calculated following Berlocher (1998) where degree of overlap equals the area of overlap divided by the smaller of the two species' ranges. Mantel tests were used to test for an association between genetic distance and degree of range overlap. If *Yucca* speciation events within the capsular-fruited and fleshy-fruited lineages occurred sympatrically, we expected a negative correlation between genetic distance and the degree of range overlap (i.e., sibling species should have low genetic distances with high degree of range overlap).

3. Results

3.1. Patterns of host use and speciation in *Tegeticula*

The *Tegeticula* clade that uses *Yucca* contains 19 named species (Supplemental Table 1). Seven of these species use capsular-fruited yuccas as hosts, nine moth species use fleshy-fruited yuccas, and two species use spongy-fruited yuccas (Supplemental Table 1). The cheater *T. corruptrix* is the only moth species that uses yuccas from more than one section, and it may best be viewed as two species based on host use and DNA sequence divergence (Segraves et al., unpublished). Twelve of the 17 pollinator species use a single yucca species (Fig. 1). *Tegeticula yuccasella* is the most polyphagous pollinator species, using seven species of yuccas (Pellmyr, 1999; Leebens-Mack and Pellmyr, 2004). The non-pollinating cheater species, *T. intermedia* and *T. corruptrix*, are known to use six yucca species each (Supplemental Table 1).

The mtDNA phylogeny for *Tegeticula* was well supported at deeper nodes, but less so for more recent divergence events (Fig. 2). There was no support for monophyly of moth species that feed on the capsular and fleshy-fruited yucca sections. The monophyly of moths on the spongy-fruited section is a consequence of the fact that this section contains a single yucca species. There have been at least two instances of host switches between capsular and fleshy-fruited yuccas within clades of pollinators. Pollinator species that use multiple yucca species, however, only use yuccas from one section. ParaFit analysis of *Tegeticula* and *Yucca* rejected the hypothesis of independence of speciation events (ParaFitGlobal = 0.01368; $P \leq 0.001$) (Fig. 2). Twenty-eight of the 40 host-parasite links were significant. There was evidence of overall co-speciation, but there are many instances of diversification in one clade without corresponding diversification in the other. JANE analyses corroborated this finding. There were 22 failure to diverge events, 24 host switching events and only 8 co-speciation events (Table 1). Changes to the cost structure for different events demonstrated that limiting the number of co-speciation events by increasing the cost ten-fold did not change the overall costs estimates for reconciliation in comparison to changes in costs for other events (Table 1).

3.2. Patterns of host use and speciation in *Prodoxus*

The *Prodoxus* clade that uses *Yucca* contains 17 identified moth species. Of these, two species use capsular-fruited yuccas as hosts, 13 species use fleshy-fruited yuccas, and two species use spongy-

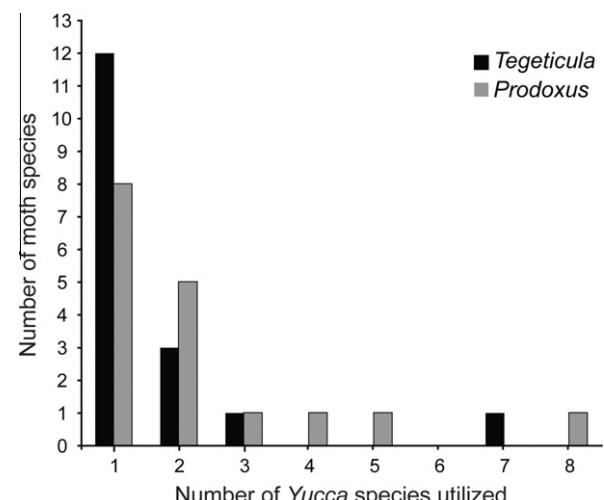


Fig. 1. Patterns of host use for *Tegeticula* pollinator moths and *Prodoxus* moths. Many species in both genera are monophagous.

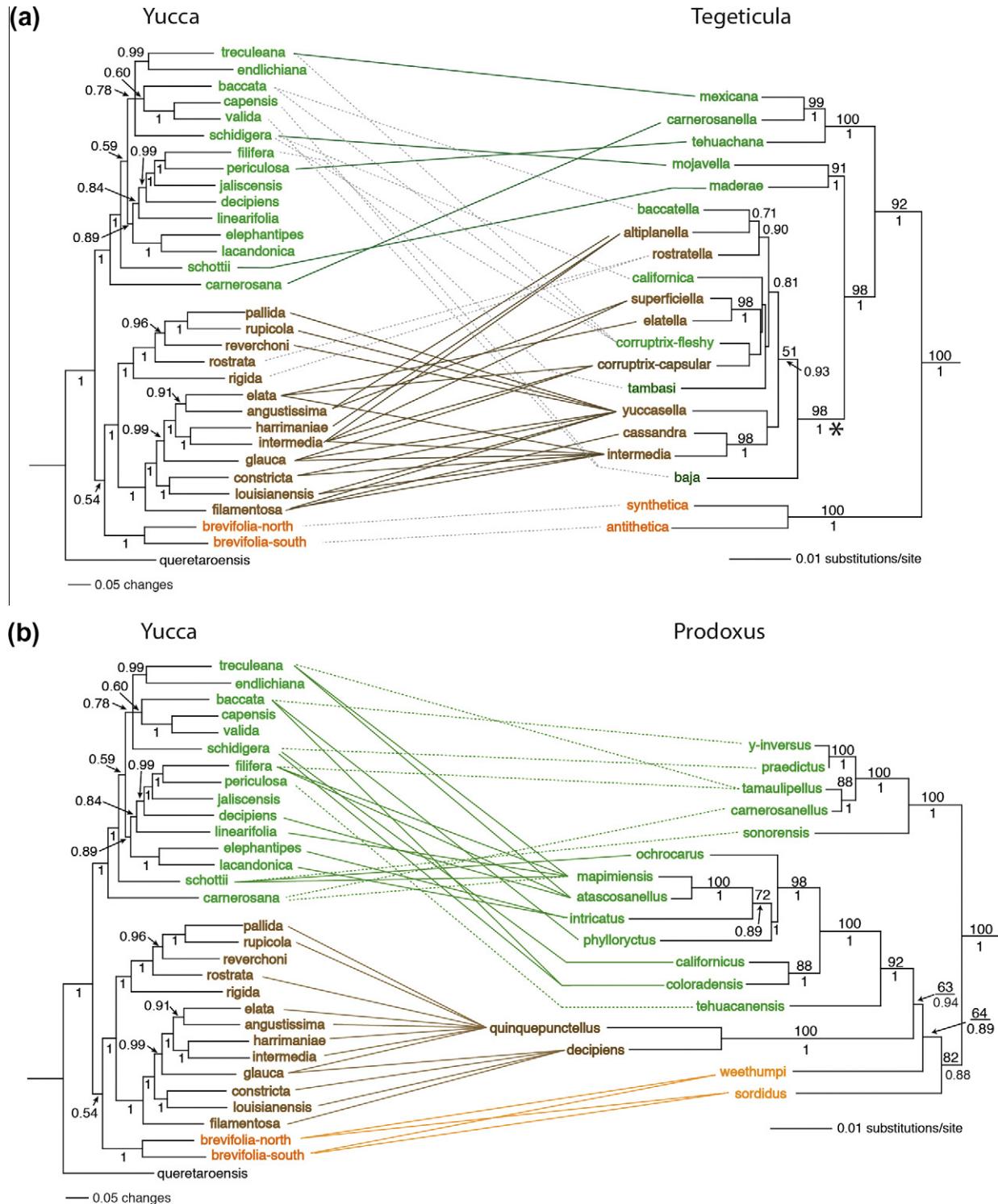


Fig. 2. Bayesian AFLP phylogeny for the plant genus *Yucca* and maximum likelihood/Bayesian cytochrome oxidase I and II mtDNA phylogeny for (a) *Tegeticula* and (b) *Prodoxus*. Numbers below the branches are Bayesian posterior probabilities and numbers above the branches are non-parametric bootstrap support values for the moth phylogenies. Names in green signify fleshy-fruited yuccas (section *Sarcocarpa*) and the moths that feed on them, names in brown signify capsular-fruited yuccas (section *Chaenocarpa*), and names in orange signify spongy-fruited yuccas (section *Clistocarpa*). The asterisk indicates the burst of speciation in *Tegeticula* approximately 3 Mya. ParaFit analysis indicated a significant overall level of co-speciation for yuccas and both moth genera. Solid lines represent significant individual co-speciation links between moth species and their hosts and dotted lines are non-significant links.

fruited yuccas. Approximately half of the moth species are monophagous and many use two yucca species (Pellmyr et al., 2006) (Fig. 1).

The mtDNA-based phylogeny for *Prodoxus* was well supported (Fig. 2). There were two monophyletic clades, one consisting of

the fruit-feeders on fleshy-fruited yuccas (*P. y-inversus*, *P. praedictus*, *P. tamaulipellus*, *P. carnerosanellus*, and *P. sonorensis*) and the other consisting of the rest of *Prodoxus*. Fleshy-fruited and spongy-fruited yuccas have fruit-feeding and stalk-feeding moths, whereas capsular-fruited yuccas are only used by stalk-feeding

moths. In contrast to *Tegeticula* there was little speciation (2 *Prodoxus* vs. 7 *Tegeticula* species) associated with capsular-fruited yuccas. ParaFit analysis of *Prodoxus* and *Yucca* rejected the hypothesis

of independence of speciation events (ParaFitGlobal = 0.06366; $P \leq 0.001$) (Fig. 2). Twenty-nine of the 37 host-parasite individual links were significant. There is evidence of overall co-speciation,

Table 1

Results of JANE co-speciation analyses for *Yucca* and *Tegeticula* and *Yucca* and *Prodoxus*. A combination of co-speciation, moth species duplication, host switching, moth species loss, and failure to diverge events were detected for each comparison. Changes to the event cost structure (default = 0, 1, 1, 2, 1) suggest that co-speciation events are not major factors in reconciliation between plant and moth phylogenies.

| Type of event | Cost scheme | Co-speciation | Duplication | Host switch | Parasite Loss | Failure to diverge | Overall cost |
|-------------------|-------------|---------------|-------------|-------------|---------------|--------------------|--------------|
| <i>Tegeticula</i> | | | | | | | |
| 0, 1, 1, 2, 1 | 8 | 24 | 12 | 3 | 22 | | 64 |
| 10, 1, 1, 2, 1 | 0 | 32 | 15 | 6 | 22 | | 81 |
| 0, 10, 1, 2, 1 | 14 | 18 | 8 | 13 | 22 | | 236 |
| 0, 1, 10, 2, 1 | 14 | 18 | 7 | 16 | 22 | | 142 |
| 0, 1, 1, 10, 1 | 8 | 24 | 12 | 3 | 22 | | 88 |
| 0, 1, 1, 2, 10 | 8 | 24 | 12 | 3 | 22 | | 262 |
| <i>Prodoxus</i> | | | | | | | |
| 0, 1, 1, 2, 1 | 6 | 26 | 6 | 41 | 40 | | 154 |
| 10, 1, 1, 2, 1 | 0 | 32 | 8 | 42 | 40 | | 164 |
| 0, 10, 1, 2, 1 | 10 | 22 | 4 | 44 | 40 | | 312 |
| 0, 1, 10, 2, 1 | 8 | 24 | 1 | 52 | 40 | | 178 |
| 0, 1, 1, 10, 1 | 4 | 28 | 7 | 40 | 40 | | 475 |
| 0, 1, 1, 2, 10 | 6 | 26 | 6 | 41 | 40 | | 514 |

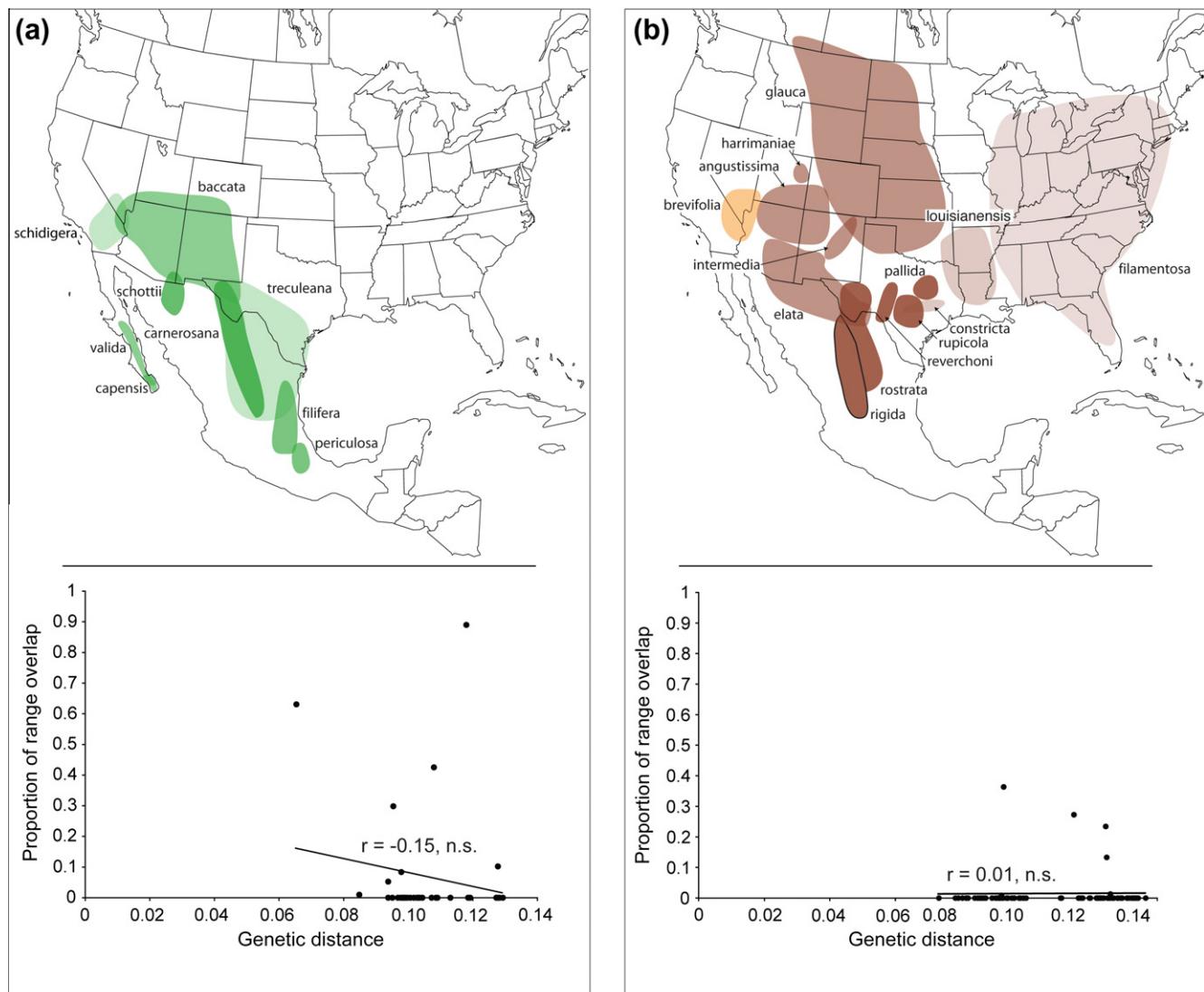


Fig. 3. Geographic distributions and correlations of range overlap with Nei-Li pairwise genetic distances of *Yucca* pollinated by *Tegeticula*. Similarly shaded ranges represent species from the same clade. (a) Ranges of fleshy-fruited yuccas (section *Sarcocarpa*) in green. Correlation, $r = -0.1565$, $P \leq 0.88$. (b) Ranges of capsular-fruited yuccas (section *Chamaecarpa*) in brown and spongy-fruited yuccas (section *Clistocarpa*) in orange. Correlation for capsular-fruited species $r = 0.11$, $P \leq 0.45$.

with few instances of independent speciation events. JANE analyses detected 40 failure to diverge events and 6 co-speciation events. As with *Tegeticula*, increasing the event cost for co-speciation ten-fold did not substantially change the total cost of reconciling the trees.

3.3. Range overlap analysis in *Yucca*

Within each subclade of the capsular-fruited and fleshy-fruited yuccas, the species ranges of *Yucca* with known *Tegeticula* pollinators are mostly allopatric (Fig. 3). For each *Yucca* section, mantel tests did not detect a significant correlation between genetic distance and percent range overlap (capsular-fruited, $r = 0.11$, $P \leq 0.45$; fleshy-fruited $r = -0.1565$, $P \leq 0.88$) (Fig. 3). *Yucca* species ranges do overlap, but these ranges are from species that are from different subclades within a section or from different sections. Species ranges from the fleshy-fruited and capsular-fruited clades overlap extensively, but within each section there is little range overlap.

4. Discussion

There is no doubt that species interactions have been an integral force in generating biodiversity (Thompson, 2005). Co-speciation analyses are one means to examine how species interactions may influence the patterns of speciation between interacting lineages. The terms co-speciation, co-diversification and coevolution have sometimes been used interchangeably, but there is an important distinction. Co-speciation and co-diversification refer to the pattern of reciprocal cladogenesis between interacting lineages, whereas coevolution is a process of reciprocal evolutionary change in response to selective pressures that interacting species impose on each other (Thompson, 1994). Interacting lineages may co-speciate or co-diversify, such as a parasites and hosts (e.g. Hafner and Page, 1995; Hughes et al., 2007), but not necessarily be coevolving. Host speciation may promote parasite speciation, as limited contact between sibling host species would isolate parasite populations as well. This process can occur in the absence of coevolution of host and parasite traits. A pattern of co-speciation may also arise in less intimately associated taxa, when geographic isolation due to climatic or geological factors affects interacting lineages similarly, resulting in concordant patterns of speciation (Segraves 2010).

Coevolution between interacting lineages has been suggested as a major process that may lead to diversification and potentially co-speciation. Ehrlich and Raven (1964) envisioned rounds of coevolution of plant defenses and insect counter-defenses leading to bursts of speciation, but not co-speciation. Thompson (1994) termed this connection between coevolution and diversification sensu Ehrlich and Raven (1964) as 'escape and radiate coevolution'. Thompson (1994) expanded on how coevolution may generate diversification by suggesting that diversifying coevolution is possible when one species controls the mating patterns of another. Diversifying coevolution has the potential to cause co-speciation between interacting lineages due to reciprocal reproductive isolation in both groups. Thompson (1994) envisioned diversifying coevolution as potentially important in plant-pollinator interactions and symbionts such as *Wolbachia* that distort sex ratios or influence mating compatibility among their insect hosts.

Obligate seed-eating pollination mutualisms are systems that seem to be likely candidates for diversifying coevolution; pollinators control the movement of male plant gametes and these systems exhibit a high degree of specificity between interacting lineages. Reproductive isolation generated by ecological or evolutionary factors in one lineage would by necessity also influence

the other lineage. Co-speciation in figs and fig wasps (Jackson, 2004; Rønsted et al., 2005; Herre et al., 2008) and *Epicephala* moths and the tree genus *Glochodion* (Kato et al., 2003; Kawakita et al., 2004; Kawakita and Kato, 2006, 2009) demonstrate that there can be co-speciation in obligate seed-eating pollination mutualisms; however, determining whether coevolution has been important in determining the patterns of speciation is more challenging. In figs and fig wasps, coevolution occurred at some point in the evolutionary history of the interacting lineages, but that does not imply that contemporary coevolution is responsible for causing speciation (Weiblen and Bush, 2002; Machado et al., 2005; Marussichi and Machado, 2007; Jackson et al., 2008; Jousselin et al., 2008; Cook and Segar, 2010).

For yuccas and pollinator yucca moths there are a number of traits that are indicative of coevolution (Pellmyr, 2003). The pollinator moths have evolved specialized mouthparts for collecting and depositing yucca pollen, and moth larvae feed exclusively on yucca species. Yuccas are solely pollinated by yucca moths and they have effectively lost the ability to produce nectar as a reward for pollinators. The presence of coevolved traits and the high degree of specificity between yuccas and their pollinator moths suggest the potential for diversifying coevolution in this interaction. In the current co-speciation analysis we can reject the null hypothesis of independent speciation. Although there are examples of host-switching and failure to diverge events in the moths, the yucca and yucca moth phylogenies exhibit concordance. Such concordance, however, does not necessarily imply the type of diversifying coevolution envisioned by Thompson (1994).

As in any co-speciation analysis, we are left with the overarching pattern, yet there remains a need to infer the process to gain a more accurate picture of the cause of diversification. Contrary to assumptions about the importance of coevolution in yuccas and yucca moths, there are multiple lines of evidence that suggest diversifying coevolution has at best, only weakly influenced speciation. For instance, one expectation of co-speciation and, in particular, of diversifying coevolution is that speciation events in interacting lineages should be nearly synchronous (Huelsenbeck et al., 2002). Molecular clock estimates for diversification events in the pollinator moths and yuccas suggest that the observed pattern of co-speciation is likely asynchronous. Estimates for the origin of *Yucca* suggest that the genus arose 18 to 9 Mybp, with the diversification of the capsular-fruited and fleshy-fruited lineages occurring 6 to 4 Mybp (Good-Avila et al., 2006; Smith et al., 2008a,b). Pellmyr and Leebens-Mack (1999) estimated *Tegeticula* had a burst of speciation (11 species) onto capsular-fruited and fleshy-fruited *Yucca* lineages 3.2 ± 1.8 Mybp. The results of these molecular clock analyses suggest that *Yucca* diversified approximately 2–3 My prior to the radiation of *Tegeticula*, although the error estimates indicate the possibility of contemporary speciation. Comparison of yucca and yucca moth tree shapes, however, does not support the hypothesis of diversifying coevolution. Whereas capsular-fruited and fleshy-fruited yuccas diverged early in the history of the genus (Smith et al., 2008a,b), all moth species currently pollinating capsular-fruited yuccas and several fleshy-fruited species arose relatively late in the history of *Tegeticula* in association with the burst of speciation mentioned above (Pellmyr and Leebens-Mack, 1999). This radiation in *Tegeticula* some three million years ago has been linked to shifts in oviposition behavior and the origin of cheating rather than coevolutionary diversification (Pellmyr and Leebens-Mack, 2000; Althoff et al., 2006). If we assume that the molecular clock estimates are accurate, it appears that pollinator moths have phylogenetically tracked yucca lineages rather than diversifying simultaneously.

A second line of evidence that suggests diversifying coevolution was weak between yuccas and yucca moths is the lack of sympatry of sibling species of plants with sibling species of pollinator moths.

Such a pattern would control for speciation caused by geographic isolation rather than by reproductive isolation driven by coevolution. A comparison of geographic range overlap and genetic distance revealed no association between relatedness and range overlap within the capsular-fruited or fleshy-fruited yucca lineages, suggesting that closely related species do not co-occur (Fig. 3). Furthermore, examination of sympatric populations indicates that there are no cases where both pollinator and yucca species are sibling species. In instances where multiple pollinator species and multiple yucca species do co-occur, the species within each group are not sibling species. In the Mojave desert, for example, the spongy-fruited *Y. brevifolia* co-occurs with the fleshy-fruited *Y. schidigera* and *Y. baccata*. Although *Y. schidigera* and *Y. baccata* are members of the same clade and it is possible that they could be sibling species, the pollinator moths that use them, *T. mojavella* and *T. baccatella*, are not sibling species and are distantly related. Similarly, Althoff et al. (2006) demonstrated that in cases where multiple capsular-fruited yucca species and their pollinators co-occur, the pollinator species are from distantly related lineages and differ in oviposition behavior.

A third line of evidence that suggests a minor role of diversifying coevolution in yuccas and yucca moths is the similar pattern of co-speciation between *Tegeticula* pollinator moths and yuccas and the non-pollinating *Prodoxus* moths and yuccas. These two equally diverse moth genera differ in the propensity for coevolution with yuccas. *Prodoxus* species do not pollinate nor do they feed on seeds. Instead they feed on other tissues and do not appear to have a significant impact on plant reproductive success (Bronstein and Ziv, 1997; Althoff et al., 2004). Even so, *Prodoxus* and *Yucca* have co-specified. This result suggests that prodoxid moths in general are likely to phylogenetically track their host plant lineages even in the absence of strong coevolution (e.g., Percy et al., 2004). If host plant traits that are important to moths were phylogenetically conserved among closely related *Yucca* species, then a moth species could colonize closely related *Yucca* species as is evident for some *Prodoxus* species. For *Prodoxus*, mating on the host plant and selection on ovipositor morphology for using different yucca species are important components for causing population differentiation at microevolutionary scales (Groman and Pellmyr, 2000; Svensson et al., 2005), which may help fuel the macroevolutionary pattern of extreme specialization in host use among moth species. In the yucca moth lineage, *Prodoxus* is more ancestral than *Tegeticula*, suggesting that *Tegeticula* may have characteristics that promote phylogenetic tracking even in the absence of coevolution.

What then is the best explanation of the non-independence of speciation between yucca moths and yuccas? The asynchrony in diversification times and the current geographical distributions of yucca and moth species suggest that much of the concordant speciation patterns may be the result of moth lineages tracking yucca lineages through time and space. If current range distributions are indicative of past ranges, then allopatric/parapatric speciation is a likely mechanism for speciation in yuccas, and, subsequently, the moths. Within the capsular-fruited yuccas, only five of the 13 species have overlapping distributions and patterns of species relatedness correspond well with biogeographic divisions (Fig. 3). For example, the clade containing *Y. glauca*, *Y. intermedia*, *Y. harrimaniae*, *Y. angustissima*, and *Y. elata* represent *Yucca* speciation in a region spanning the Colorado Plateau, the Great Plains, and the desert regions of the southwestern United States and northern Mexico. Similarly, within the fleshy-fruited yuccas that are pollinated by *Tegeticula*, there are few overlapping ranges. The range of *Y. carnerosana* is within the range of *Y. treculeana*, but these are distantly related taxa and the pollinators that use them are also distantly related (Fig. 3). The geographic template of *Yucca* species distribution served as the foundation for moth speciation events. Thus, yuccas exhibit a pattern of speciation that is

consistent with biogeographic separation as do the *Tegeticula* and *Prodoxus* species that use them (Althoff et al., 2006; Pellmyr et al., 2006).

The issue of using current range distributions to infer speciation patterns has a long history in evolutionary biology (e.g. Mayr, 1942; Brooks and McLennan, 1991; Morrone, 2009). Relatively recently however, Losos and Glor (2003) raise valid concerns about interpreting the geographical mode of speciation in a phylogenetic context based on current distributions. In particular they argue that species distributions can change drastically over evolutionary timescales and that it is difficult to infer species ranges at the time of speciation event. Given the large geographic range of *Yucca* and the complex historical biogeography of North America (Graham 1999) attempting to infer the historical range distribution of each *Yucca* species is problematic at best. We suggest, however, that the alternative scenario of coevolution between pollinators and yuccas causing repeated sympatric speciation events followed by numerous range contractions is highly improbable given the number of times that this would have had to occur to generate the present patterns. A simpler and more probable scenario is that moth lineages have phylogenetically tracked *Yucca* lineages through time and space. Moths are able fliers and have a much greater dispersal capacity than *Yucca*, allowing them to colonize new species of plants in different biogeographic regions (Leebens-Mack and Pellmyr, 2004). Coevolution is ongoing between some yuccas and pollinator moths at local scales (Smith et al., 2008a,b; Godsoe et al., 2008; Smith et al., 2009), but coevolution is unlikely to have caused the observed large-scale patterns of co-speciation.

Because of the high degree of allopatry among closely related yuccas, the interpretation of host use patterns of *Tegeticula* and *Prodoxus* in relation to plant phylogeny is confounded by geography as well. That is, current levels of host specificity may be an artifact of biogeography rather than (co-) evolutionary specialization to a particular *Yucca* species. This is supported by the fact that some pollinator species are capable of using multiple yucca species within a given area and moth ranges are less constrained than plant ranges. *Tegeticula altiplanella* and *T. superficiella* both use the capsular-fruited yucca species that occur in the Colorado Plateau region (Althoff et al., 2006). The most polyphagous pollinator species, *T. yuccasella*, uses yucca species across eastern North America and the Edwards Plateau in central Texas (Pellmyr, 2003; Leebens-Mack and Pellmyr, 2004). In *Prodoxus*, the two species that use capsular-fruited species, *P. decipiens* and *P. quinquepunctellus*, are quite polyphagous and have host ranges that segregate into eastern yucca species and western yucca species, respectively (Althoff et al., 2001). *Prodoxus mapimiensis* appears to have incorporated many yucca species that are circumscribed by the range of *Y. treculeana* (Pellmyr et al., 2006). There is a high degree of monophagy for both moth groups, but much of this may be driven by ecological opportunity rather than differential selection pressures associated with different species of *Yucca*. Many of the geographic ranges of closely related yucca species do not overlap so there is no opportunity for moths to encounter additional phylogenetically-similar host plant species.

Given that there is little support for diversifying coevolution between yuccas and their pollinators, the question remains as to the underlying forces driving speciation in yuccas. If yuccas must have a moth pollinator that moves pollen, how were yuccas able to diversify in allopatry without corresponding diversification in the pollinators? This diversification is particularly puzzling since plant reproductive isolation implies that moth dispersal patterns were restricted as well. The lack of concordance of plant and moth diversification timing suggest that yuccas diversified first, followed by a later radiation of *Tegeticula* pollinators that replaced or complemented existing pollinators. Since yuccas require the pollination services of moths, another group of moths that could have initially

filled this role is *Parategeticula*. *Parategeticula* is the only other genus known to pollinate yuccas (Davis, 1967; Powell, 1984; Pellmyr et al., 2008). There are only five recognized species of *Parategeticula*, all of which occur only in the southern portion of the extant range of *Yucca*, which is the area suggested to be the origin of the genus *Yucca* (Clary, 1997). A possible hypothesis consistent with available phylogenetic data and molecular clock estimates is that *Parategeticula* preceded *Tegeticula* as specialized pollinators of yuccas (Pellmyr and Leebens-Mack, 1999). *Parategeticula* are poor fliers compared to *Tegeticula*, having lost the wing-locking mechanism that facilitates strong flight in lepidopterans. Their reduced flying ability may have facilitated reproductive isolation among yucca populations, and also made the moths more susceptible to extinction especially during glacial cycles. As yucca ranges expanded and contracted, some *Parategeticula* may have become extinct in parts of the host plant range and were replaced by *Tegeticula*.

In conclusion, it may be impossible to fully reconstruct the evolutionary reasons for the pattern of speciation in the yucca–yucca moth obligate mutualism, but currently available data strongly suggest that diversification in both lineages was not driven primarily by coevolution. The large degree of allopatric speciation in closely related plant and moth taxa, the incongruence of timing of speciation events in each lineage, and similar levels of co-speciation in non-pollinating yucca moths and yuccas indicate that other factors were more important. Pollinators in the genus *Tegeticula* likely radiated onto an already existing template of yucca diversification that was delimited by biogeography.

Acknowledgments

This research is partly due to many individuals who assisted with specimen collection and data collection. The authors thank in particular Don Davis and Jerry Powell for sharing their vast experience with yucca moths and providing the phylogenetic and systematic framework on which this research was originally based. Jeremy Yoder helped in sequence data collection for *Prodoxus predictus*. The Florida Park Service, Ocala National Forest, The Nature Conservancy at Apalachicola Bluffs, Archbold Biological Station, Big Bend National Park, Black Gap Wildlife Management Area, Jornada Long-Term Ecological Research site, Mojave National Preserve, Torrey Pines State Reserve and White Sands National Monument provided permits and access to field sites. The manuscript was improved significantly by anonymous reviewers who provided many insightful comments and suggestions. We thank K. Glennon, E. Carter, and N. Schwarting for discussion and comments on the manuscript. Financial support was provided by NSF grants DEB 0321293 to Pellmyr and Althoff, DEB 0516841 to Pellmyr and Smith, and DEB 0743101 to Segraves and Althoff.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.11.024.

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